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### CURRENT UNDERSTANDING OF THE MECHANISMS OF HEAT STRESS TOLERANCE IN RICE (*Oryza sativa* L.)

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#### KEYWORDS

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Tolerance

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#### ABSTRACT

Various studies reported by scientific communities such as NASA's Goddard Institute for Space Studies (GISS) indicated an increase in average global temperature by approx. 0.8 °C since 1880. Rice (*Oryza sativa* L.), a heat sensitive plant cereal crop could be greatly affected by heat stress due to global temperature rise. Thus, it is envisaged that rice productivity could markedly decrease due to a rise in mean atmospheric temperature. Different studies have been reported possible mechanisms of heat stress tolerance in Rice. The present review will therefore discuss the current fundamental understanding of heat tolerant mechanisms involving heat shock proteins, plant hormones, plant growth regulators, osmoprotectants, and the importance of membrane thermal stability in rice.

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## 1 Introduction

Heat tolerance can be defined as the ability to undergo normal plant growth and to produce normal yields when exposed to heat stress (Yamanouchi et al., 2002; Wahid et al., 2007). Understanding the physiological mechanisms underlying heat stress response and tolerance in plants is of utmost importance in the present context of an increase in global temperature (Fahad et al., 2017; Prasad et al., 2017; Govindaraj et al., 2018). Figure 1 suggested that heat stress causes adverse effects on the growth and development of plants, ultimately affecting the yield of the crop plant (Hasanuzzaman et al., 2012; Hasanuzzaman et al., 2013). High temperature stress during reproductive or grain-filling stages is shown to have negative effects on grain quality and yield (Bahuguna et al., 2015). The photosynthetic process was found to be negatively affected when rice plants were exposed to a temperature of 3.6°C - 7.0°C higher than critical temperature (Oh-e et al., 2007; Fahad et al., 2016a). Based on the prevailing world food crisis and present understandings of the unwanted impacts of the rise in global temperature on cereal crops, there is an urgent need to understand the various approaches and mechanisms to address heat stress and to develop new heat-tolerant rice cultivars to cope with these problems. Various studies have implicated the importance of scavenging reactive oxygen species, maintaining the normal structure and functionality of enzymes and proteins for efficient heat stress tolerance (Maestri et al., 2002; Lei et al., 2018). Thus, with the ever-increasing need to meet the global food crisis it becomes imperative to properly decipher various mechanisms to address temperature stress in rice plants.

Heat stress leads to degradation of Rubisco, thereby affecting plant photosynthetic process and yield. It also causes spikelet sterility and leads to reduce in reproduction in rice. Apart from many other damages, it causes reduce in auxin level which is required for maintaining spikelet fertility, reduces membrane stability, and causes electrolytic leakage, thereby causing a decline in seed set and yield.

## 2 Avoidance mechanisms

High temperature mostly affects rice plants during the anthesis, i.e. at the time of opening of flowers, thereby decreasing the fertility of the spikelet. Exposure to high temperatures for one hour has been reported to induce spikelet sterility. However, various studies have also indicated that after one hour of flowering, the spikelets are less affected by exposure to high temperatures (Satake & Yoshida, 1978; Jagadish et al., 2007; Julia & Dingkuhn, 2012). Thus, spikelet sterility could be an important trait to study rice genotypes for their ability to tolerate heat stress (Weerakoon et al., 2008). Early morning flowering when the air temperature is cooler is a useful trait that reduces spikelet sterility (Yoshida, 1981). Thus, understanding genes that control anthesis and flowering time is of utmost importance to decipher the mechanism of heat stress tolerance. Similarly, genes responsible for early flowering can be studied to explore various possible mechanisms for imparting heat tolerance in rice (Sheehy et al., 2005; Bheemanahalli et al., 2017). Studies have indicated a close relationship between spikelet fertility and panicle temperature (Julia & Dingkuhn, 2013), and suggested that one avoidance mechanism for heat stress is by

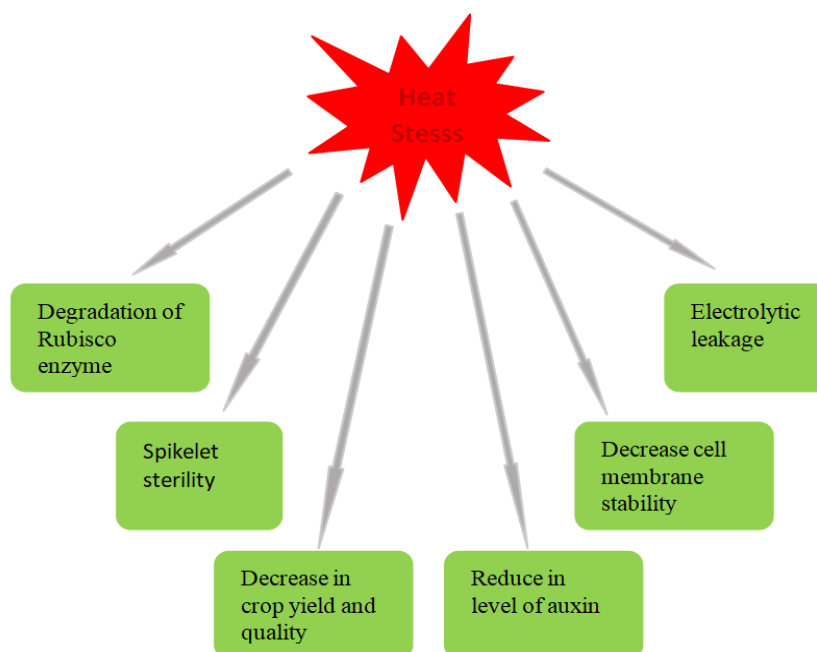


Figure 1 Some of the detrimental effects of heat stress in rice plant.

lowering panicle temperature by transpirational cooling (Xiong et al., 2014), and rice plants can decrease the panicle temperature up to 10 °C by transpiration, and thereby helps in maintaining spikelet fertility. Thus, rice plants that have longer and erect top leaves help in protecting the panicle from direct sunshine, and thereby confer heat tolerance.

### 3 Tolerance mechanisms

The ability to tolerate heat in rice is different for different species and cultivars, even different organs and tissues of a plant may exhibit varying abilities to tolerate heat stress. Various studies have reported the role of heat shock proteins, plant hormones, osmoprotectants, and membrane thermal stability in this regard.

#### 3.1 Role of heat shock proteins (HSPs)

The synthesis and accumulation of HSPs is a prompt response after exposure to high temperatures and it is considered as one of the most important adaptive strategies to overcome the deleterious effects of heat stress. The fast build-up of HSPs in soft tissue plays important role in conferring thermostability at the cellular level; thereby promote plants to perform better under heat stress conditions (Wahid et al., 2007; Keller & Simm, 2018). Heat shock factors (Hsf), which are the transcriptional activators of HSPs, and HSPs have been reported for their roles in various types of abiotic stresses including heat stress. HSPs prevent the accumulation of proteins with anomalous conformations and eliminate non-native aggregations formed during stress with ubiquitin-mediated degradation of these proteins (Kotak et al., 2007). It is predicted that heat tolerance and heat shock proteins (HSPs) production are closely related (Huang & Xu, 2008).

Transgenic rice inserted with HSP101 from *Arabidopsis thaliana* cDNA indicated the important role of HSP in enhancing heat stress tolerance. The transformed transgenic rice showed the ability to undergo normal growth and development as compared to their untransformed counterpart (Katiyar-Agarwal et al., 2003). The expressions of HSPs in anther were also found to be elevated in heat stress-tolerant rice variety. Such variety showed higher spikelet fertility (Jagadish et al., 2010). Thus, the ability to express more HSPs is an important heat stress tolerance mechanism in rice (Chang et al., 2007), and a deeper understanding of the elevated production of HSPs is of great significance for alleviating heat stress.

#### 3.2 Role of plant hormones and plant growth regulators

Different plant hormones and plant growth regulators are reported for their protective roles against heat stress in rice plants. Studies on exogenous application of plant hormones and plant growth regulators (PGR) on rice indicated important roles of ascorbic acid, alpha-tocopherol, salicylic acid (SA), glycine betaine (GB), auxins,

brassinosteroids (BRs), and methyl jasmonates (MeJA) in ameliorating the adverse effects of high temperature stress (Mohammed & Tarpley, 2011; Fahad et al., 2016b). Thus, understanding how these plant hormones function will be of great help in the overall search for mechanisms of high temperature tolerance in rice plants.

Salicylic acid has been reported for its role in the regulation of various physiological processes in plants in response to abiotic stresses (Hayat et al., 2010). Under heat stress, exogenous application of salicylic acid (1 and 10 mmol L<sup>-1</sup>) could lead to higher grain yield, spikelet number per panicle, and setting rate (Zhang et al., 2017). This study even suggested the roles of IAA, sugars, and antioxidant enzymes along with SA in avoiding spikelet degeneration. Salicylic acid treatments in rice also lead to induction of Class II HSP (*Oshsp18.0*) (Chang et al., 2007). Another study showed that the application of SA resulted in increased antioxidant capacity, thereby avoiding membrane damages in rice plants (Mohammed & Tarpley, 2011).

Various studies have reported the ability of methyl jasmonates (MeJA) in advancing the flowering time in the morning, which is an important mechanism to mitigate heat stress. Studies on the effects of MeJA on rice floret opening indicated that it significantly induces the opening of rice florets within about 30 min, with the most rapid induction occurring just 6 min after treatment. The numbers of induced opening florets are correlated with MeJA concentrations. Higher concentrations of MeJA induced more florets (Zeng et al., 1999). Another study showed that the application of MeJA resulted in the opening of flowers within 80 mins. It also resulted in advancing the time of flower opening by two hours and also led to an increase in the opening of more flowers, which were supposed to be opened the next day (Kobayasi & Atsuta, 2010).

Studies on the relationship between heat stress tolerance and Brassinosteroids (BRs) signaling showed that disruption of the gene brassinosteroid insensitive 2 (BIN2) that encodes for a negative regulator of the BRs receptor Brassinosteroid Insensitive 1 (BRI1) leads to increase tolerance to a variety of abiotic stress including heat shock (Koh et al., 2007). Brassinosteroid's application resulted in a higher accumulation of major heat shock proteins and several translation initiations and elongation factors and could maintain the net photosynthetic rate, enhanced stomatal conductance, stomatal limitation, and water-use efficiency (Dhaubhadel et al., 2002; Sonjaroon et al., 2017). Brassinosteroids application also has been reported to stimulate stress tolerance by positively regulating the synthesis of endogenous hormones, such as indole-3-acetic acid, zeatin riboside, jasmonic acid, brassinosteroids, and gibberellic acid (Anwar et al., 2018). Foliar application of 24-epibrassinolide (0.5, 1, and 1.5 ppm) on rice cultivars (Pusa Sugandh 5 and Nerica L 44) showed a strong

positive relationship between grain yield and leaf photosynthesis. The foliar application of brassinosteroid, salicylic acid, and calcium (calcium chloride) has been suggested to ameliorate the decrease in PSII efficiency at pre-anthesis in rice (Chandrakala et al., 2013).

The reproductive stage in rice requires an optimum level of hormones like auxin and other energy-producing compounds. Naphthalene acetic acid (NAA) applied immediately after flowering improved the crop tolerance to heat stress which leads to better crop productivity. The decrease in rice crop yield and quality due to heat stress can be controlled with optimum level (20  $\mu\text{mol L}^{-1}$ ) of exogenous application of Naphthalene acetic acid (NAA) (Naeem et al., 2019). Auxin also plays an important role in maintaining spikelet fertility. The reduced level of active IAA could cause pollen abortion and male sterility. High temperature could also lead to a reduction in the level of auxin (Sonjaroon et al., 2017). Spraying of naphthaleneacetic acid could stop the reduction of pollen tube growth and could reverse the spikelet sterility in rice (Zhang et al., 2018).

A study using L-galactono-1,4-lactone dehydrogenase overexpressed (GO-2) and L-galactono-1,4-lactone dehydrogenase suppressed (GI-2) transgenic rice as experimental materials showed that application of ascorbic acid resulted in significantly lowered maximal quantum yield of photosystem II ( $\Phi\text{PSII}$ ) in GI-2, and higher in GO-2 compared to wild type rice, whereas the content of reactive oxygen species (ROS) was the highest in GI-2, thereby suggesting that higher ascorbic acid content reduced the accumulation of ROS and maintained the function of rice leaves. Thus, it is believed that high ascorbic acid content could improve the rice resistance to high-temperature stress (Zhang et al., 2018).

#### 4 Role of osmoprotectants

Heat stress in plants leads to adaptive accumulation of various types of osmoprotectants such as glycine betaine, trehalose, and proline, which are not deficient in heat stress-sensitive plants. Thus, it is suggested that exogenous application or inherent ability to accumulate these osmolytes could help plants in tolerating heat stress (Jain et al., 2001; Rasheed et al., 2011; Sakamoto & Murata, 2002). These solutes play important role in the osmotic adjustment and maintain the water contents and protect leaf cells under abiotic stresses, especially under drought and heat stress. Lower production of osmoprotectants under heat and drought stress could expedite the assaults by ROS, thereby leading to senescence of leaves.

Glycine betaine (GB) is an important osmolyte that helps in imparting heat stress tolerance in plants (Sakamoto & Murata, 2002). It has been reported for its role in protecting heat degradation of Rubisco, citrate synthase, and other enzymes

(Mäkelä et al., 2000). Under high temperature stress, many plants could accumulate glycine betaine, but rice and many other plants cannot do so. Thus, exogenous application of glycine betaine could increase yields under high temperatures, possibly by enhancing antioxidant levels, which might have protected the enzymes and membranes from degradation (Quan et al., 2004; Mohammed & Tarpley, 2011; Annunziata et al., 2019). The application of glycine betaine could also help in preventing the Rubisco enzyme from being degraded (Dionisio-Sese et al., 2000). Glycine betaine has also been reported for its ability to enhance the rate of pollen germination and increase spikelet fertility.

Accumulation of proline under heat stress has been reported to help plants in osmotic adjustment (Szabados & Savoure, 2010). A study reported that plants with higher content of proline were observed to be less affected by both heat and drought stress as compared to those plants with lower proline content (de Ronde et al., 2004). However, the effect of proline is not independent but relies on many factors, one among them being phytohormones. Brief exposure of rice plants to high temperatures resulted in the rise in proline levels, which is indicative of heat stress (Tang et al., 2008). Rice genotypes that could adapt more efficiently were reported to have more proline content (Ahmed & Hasan, 2011). Application of proline lowered the Malondialdehyde (MDA) content in rice, which may be due to its ability to increase the antioxidant defense system (Nounjan et al., 2012).

Spermidine (Spd), a widely distributed polyamine has been reported for its adaptive role in heat stress in plants (Das et al., 2014). Most studies have implicated that its antioxidant capacity and ability to reduce the rate of superoxide anion and malondialdehyde (MDA) could have attributed towards its ability to maintain membrane stability under environmental stress (Farooq et al., 2009; Tian et al., 2009). Exogenous application of Spd was shown to cause reduction of propionaldehyde, hydrogen peroxide, and proline contents in rice seedlings, but lead to an increase in glutathione, ascorbic acid, fresh weight (FW), and chlorophyll contents (Mostofa et al., 2014). A comprehensive study showed that Spd could help protect PS II by its ability to increase the light energy used in the photochemical reaction,  $F_v/F_m$  ( $F_v$  = variable fluorescence;  $F_m$  = maximum),  $\Phi\text{PSII}$  (quantum yield of PSII photochemistry =  $\Phi\text{PSII}$ ), and ETR (relative rate of electron transport = ETR). These findings indicated that Spd could have brought about optimization of energy distribution and prevented damages to the structure of the photosynthetic system, and help in the proper functioning of the photosynthetic system. Another study showed that Spd might help in reducing leaf temperature by increasing the rate of transpiration rate and by preventing membrane damage. Spd spraying on two rice species (japonica rice varieties Wuyunjing 24 and Ningjing 3) could significantly promote the rate of seed-setting and grain weight. Exogenous application of Spd also could effectively prevent

damages caused by heat stress on the photosynthetic systems, antioxidants, and osmotic balance, and could enhance the cellular defense capability. Moreover, it was shown to help in maintaining a temperature suitable for seed-setting rate and grain weight by improving transpiration rate and stomatal conductance, thereby lowering the leaf temperature during heat stress (Tang et al., 2018).

### 5 Role of membrane thermal stability

Membrane thermostability is an important reliable trait that can be used to screen out the tolerant rice genotypes (Sailaja et al., 2015). The cell membrane is one of the main cellular targets to different stresses and maintenance of membrane stability during stress is important for normal physiological metabolism to continue (Levitt, 1980). Cell membrane stability or the reciprocal of cell membrane injury is an important indicator of the ability of a plant to tolerate drought and temperature stress (Sullivan, 1972; Blum & Ebercon, 1981; Forkar et al., 1988; Sadalla et al., 1990; Reynolds et al., 1994). Thus, the extent of its damage is commonly used as a measure of tolerance to heat and drought.

Electrolytic leakage expressed as relative injury measured at an early grain-fill (EGF) stage was greater in plants grown under high nighttime temperature (HNT) (32°C) compared with the plants grown under ambient nighttime temperature (ANT) (27°C). On average, plants grown under HNT showed a 60% increase in electrolytic leakage compared with plants grown under ANT. Application of vitamin E, glycine betaine, and salicylic acid decreased electrolytic leakage by 31, 42, and 30%, respectively, compared with untreated plants grown under ANT. Membrane

thermal stability, when measured as the conductivity of electrolytes leaking from leaf disks at high temperatures, has been suggested as one of the best techniques to evaluate the performance of a plant under high temperatures. Therefore, decreased membrane stability in plants grown under HNT indicated that high temperatures lead to leaky membranes. Application of GB or SA could lead to increased antioxidant capacity that can reduce oxidative damage, thereby increasing membrane thermal stability and reducing leaf dark respiration rates (Abdul-Razack & Lee, 2009). Thus, GB and SA can be used as exogenous effectors to ameliorate the effects of HNT. Both compounds increased the total antioxidant capacity of the rice plant, thereby presumably decreasing the leaf dark respiration rates and electrolytic leakage, hence increasing the yield. Genetic variability for membrane thermostability revealed that membrane thermostability showed a high positive direct effect along with positive genetic correlation on grain yield per plant next to the major yield contributing trait number of productive tillers per plant. Hence, genotypes that have high membrane thermostability, low relative injury offer scopes for direct selection/hybridization for future elaborate investigations on high temperature tolerance in rice (Maavimani et al., 2014).

It can be drawn from some of the above mentioned roles of HSPs, plant hormones, plant growth regulators, osmoprotectants, and thermal stability that heat tolerance in rice involves different mechanisms that account for the ability of plants to tolerate adverse effects of heat stress (figure 2). Explicit understanding of these mechanisms and how they relate to one another is of great importance for successfully encountering heat stress in rice.

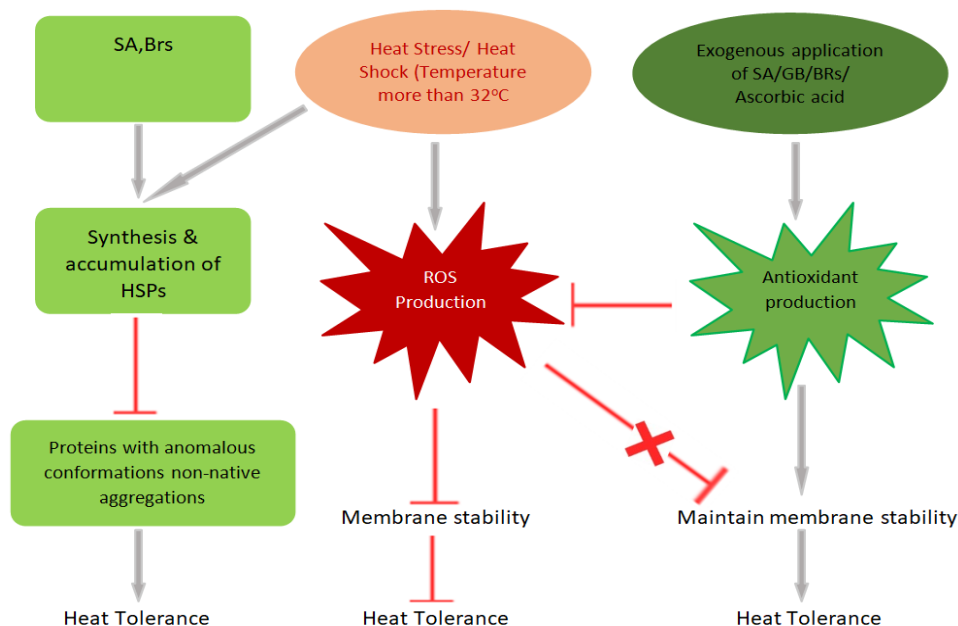


Figure 2 Some possible mechanisms to ameliorate heat stress in rice

Heat stress (temperature more than 32°C) resulted in the induction and synthesis of HSPs in some rice plant species. The HSPs helps in the elimination of proteins with anomalous conformations, as well as eliminate proteins with nonnative aggregations, thereby helping the plant in coping with the heat stress effects. Synthesis of HSPs can be induced by exogenous application of Salicylic acid (SA) and Brassinosteroids (Brs). Heat stress can lead to an increase in the accumulation of reactive oxygen species (ROS) which can decrease and damage membrane stability, leading to a decline in plant growth and productivity. Exogenous application of SA, Glycine betaine (GB)/ Brassinosteroids (Brs), and Ascorbic acid help in the production of antioxidants that help in maintaining membrane stability and heat stress tolerance in rice.

### Conclusions

Heat stress can damage most of the physiological processes of growth and reproduction in rice. As an increase in global temperature has become a reality, it has become more important to expedite our understanding of the mechanisms to face the global issue of food crisis. Hence, the present scenario demands a clarion call to all the scientific communities to look for different measures to understand heat tolerance mechanisms to produce plants that can produce optimal yields under harsh environmental conditions. Understanding every mechanism will help us in selecting the best traits and interventions to encounter heat stress. It is suggested that a deeper understanding of the roles of various desirable traits and roles of hormones, plant growth regulators, HSPs, and osmoprotectants, complemented with genetic modification and breeding techniques will greatly help in effective dealing of heat stress problems.

### Conflicts of interest

Nil

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